NURSERY PERFORMANCE OF BLACK WALNUT (JUGLANS NIGRA L.) TWINS

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ABSTRACT

Black walnut twins were obtained by splitting germinating nuts. Estimates of variance components were based on nursery performance among half-sib families, among twins and within twins. The environmental component accounted for about one-half of the total variation for date of leaf fall, diameter and height growth. Genetic variance due to additive gene action was very high. Half-sib family selection and breeding are recommended for black walnut.

Additional key words: Half-sib progeny testing, genetic variation, combining ability.

INTRODUCTION

The choice of whether to use controlled- or open-pollinated breeding methods depends on the relative gains due to specific and general combining ability as well as the relative costs associated with making these gains. General combining ability (GCA) can be estimated by half-sib progeny tests whereas it takes a full-sib test to estimate specific combining ability (SCA). GCA is the result of additive effects (A) and epistatic effects due to additive gene combinations (AA). SCA is the result of dominance effects (D) and epistatic effects due to dominance gene combination (AD, DD). It follows that we have a variance (V) for each as:

$$V(GCA) = F\, V_A + F^2\, V_{AA} + \ldots \qquad (1)$$

$$V(SCA) = F^2 V_D + F^3\, V_{AD} + F^4\, V_{DD} + \ldots \qquad (2)$$

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where F = inbreeding coefficient of the next inbred generation (Falconer 1960).

Genetic components can be separated using elaborate controlled crossing procedures (Comstock and Robinson 1948). However, because controlled crossing in black walnut is difficult and expensive, we have chosen another method to get the information. In this study, we have obtained genetically identical pairs (twins) of black walnut trees from half-sib progenies for evaluation. The objective of this study is to compare the merit of genetic gains for various traits in black walnut from open- and controlled-pollination breeding methods.

METHODS

In the fall of 1971 about 100 seeds were collected from each of 23 black walnut trees in a three-county area in southern Illinois. The seeds were stratified over winter. In the spring the seeds were placed in a warm room and allowed to germinate. When the radicle had extended about 1 cm, the radicle and epicotyl were split longitudinally using a razor blade (Bey 1967). Each half of the genetically identical pair was put in a pint-size milk carton filled with fine sand and placed in a greenhouse. When both halves of the pair were about 10 cm tall, they were planted in a nursery at a 30 x 30 cm spacing in 4 randomized blocks. Lack of sufficient germination prohibited use of all families. On the other hand, extra germinated pairs which were planted on the fifth block were not used in this analysis. These extra seedlings were used later as border trees in the outplanting.

In comparison to the common half-sib progeny test, this procedure yields about 70% more seedlings. The probability of a successful splitting was better than 95% and the probability of survival for both split twins was better than 90% in the greenhouse and in the nursery.

Additional time for this procedure involved about 30 man-hours for the splitting, potting the seedlings, and transplanting in the nursery.

Data were collected on date of leaf fall, height, and diameter at the end of the growing season. Leaf fall was defined as the date when at least all but one of the leaves on the seedling had fallen.

ANALYSIS

The analysis of variance model was used to estimate the genetic and environmental effects for the various sources of variation. The source of variation, degrees of freedom (df) and expected mean square (EMS) are as follows:

Source	df	EMS
Block	3	$V_e + 2V_s + 11.58V_{bf} + 186.46V_b$
Family	15	$V_e + 2V_s + 11.58V_{bf} + 46.43V_f$
B x F	45	$V_e + 2V_s + 11.58V_{bf}$
Seed/B x F	309	$V_e + 2V_s$
Within Seed	373	V_e
Total	745	

Assuming that the higher order interactions of the genetic components (V_{AA}, V_{AAA}, V_{AD}, V_{DD}) are insignificant, we have

$$V_s = 3/4\ V_A + V_D \tag{3}$$

$$V_f = 1/4\ V_A \tag{4}$$

$$V_G = V_s + V_f = V_A + V_D \tag{5}$$

The mean squares for the various sources of variation were equated to the expected mean squares. By simultaneously solving these equations, we computed the V_e, V_s, V_{bf}, V_f, and V_b. With the V_s and V_f known, and using equations (3) and (4), we solved for the V_A and V_D.

Heritability was computed using the following equations:

$$h^2 \text{ (narrow sense)} = \frac{V_A}{V_e + V_b + V_{bxf} + V_f + V_s}$$

$$h^2 \text{ (broad sense)} = \frac{V_A + V_D}{V_e + V_b + V_{bxf} + V_f + V_s}$$

RESULTS

Gene action.--Genetic variance due to additive gene action was very high. For the three traits evaluated we obtained the following values:

	Percent of total phenotypic variance	Percent of total genetic variance
Height	40	92
Diameter	37	100
Leaf fall	45	100

Variance components.--The environmental component ($V_b + V_e$) accounted for about one-half of the total variation for each trait (Table 1). The seed component was generally three times as large as the family component, while the block x family component was smallest of all and quite insignificant. The block component for date of leaf fall was very small compared to height and diameter. Conversely, the error variance for blocks was higher than for height and diameter.

Heritability.--Heritability values for the three traits were as follows:

	Narrow sense	Broad sense
Height	.40	.43
Diameter	.37	.37
Leaf fall	.45	.45

Table 1.--Variance components for the first-year height, diameter and date of leaf fall.

Source	Component	Trait		
		Height	Diameter	Leaf fall
Environment	V_b	.35	.30	.05
	V_e	.19	.29	.43
G x E	V_{bxf}	.03	.04	.07
Genetic	V_f	.10	.10	.12
	V_s	.33	.27	.33

These heritabilities correspond closely with others reported by Bey et al. (1971).

DISCUSSION

According to equations (3) and (4), the variance component for seed within family and block (V_s) should be equal or greater than three times the magnitude of the family component (Vf). However, for diameter and date of leaf fall, the V_s was less than $3Vf$. Consequently, we have to use formula (5) to compute the total genetic variance and to report V_a as 100 percent. Otherwise, we would have a negative VD by solving formulas (3) and (4) simultaneously. One interpretation of a negative VD is that there is a sampling error in both V_s and V_f. The mean + 1 standard deviation for V_s and Vf in diameter are 1.95 + .25 and .68 + .31, respectively; and in date of leaf fall, 16.9 + 2.39 and 6.2 + 2.87, respectively. Thus, the probability of obtaining a V_s value less than 3 Vf seems quite probable.

However if we can assume that no sampling error has occurred, then we offer another interpretation. The coefficients for VA in formulas (3) and (4) may not be true because of limited number of pollinators. Half-sib family variation accounts for 1/4 of the additive genetic variance if there are infinite and unrelated male parents. Otherwise the coefficient for V_A would be greater than 1/4. Because black walnut generally occurs as scattered individuals and we assume the mother tree usually receives most of the pollen from a few close neighbors, the inbreeding coefficient would not be equal but greater than one-fourth. If we assumed that no dominance variation is present, the intra-family correlations (0) can be estimated as $Vf/(Vf + V_s)$. In this study, the intra-family correlation plus and minus one standard deviation are .260 + .090 and .268 + .129 respectively for diameter and date of leaf fall.

Under the assumptions of random mating and related male parentage we have 0 = .25 + 1/(4 x No. of neighboring pollinators). Therefore, one can compute the number of outside pollinators from various values of 0.

The cumulative probability of obtaining pollen from more than the indicated number of neighboring pollinators is shown by figure 1. For example, the probability of obtaining pollen from more than 14 neighbors is .5; as estimated from date of leaf fall. Based on both traits, about 42 percent of the pollen comes from 1 to 10 pollinators. If it is true that no dominant variation exists for the two traits and that pollen comes from related parents, then black walnut breeders should expect no significant inbreeding depression. In fact, with 100 percent additive gene action some inbreeding may be beneficial. This is based on our assumption that the breeding scheme in wild populations is at its adaptive peak.

In this early study where gene action for diameter growth and date of leaf fall are additive, we can expect specific combining ability (SCA) to be twice that of general combining ability (GCA). For a given selection differential, the gain for full-sib family selection would equal twice that of the half-sib family selection. A small amount of dominant variation (3% of the phenotypic or 8 of the genetic variation) was found in height growth. This gives a SCA to GCA ratio of 2.09 to 1.0.

Although it is possible to make controlled crosses in black walnut, it has not been very successful. Walnut female flowers occur on the tip of new growth and usually in clusters of two. For each pollination bag that is applied to a tree, the best we could hope for would be two nuts. Even without any specific cost figures, it is easy to see that walnut controlled pollination techniques would be very costly.

It seems most logical that we should use half-sib rather than full-sib progeny testing to discover genetic variation for the black walnut improvement. In the first few generations, moderate gain (5% to 100) can be obtained from half-sib family selection.

The variation between identical twins (V_e) is approximately equal to the variation among twin pairs (V_s) within a family (half-sib progeny). Although results in twin study are not as precise as in twin cattle experiments, it does offer us a valuable alternative for estimating some genetic parameters without making controlled pollinations. We have outplanted the seedling twins and will take further observations on their performance

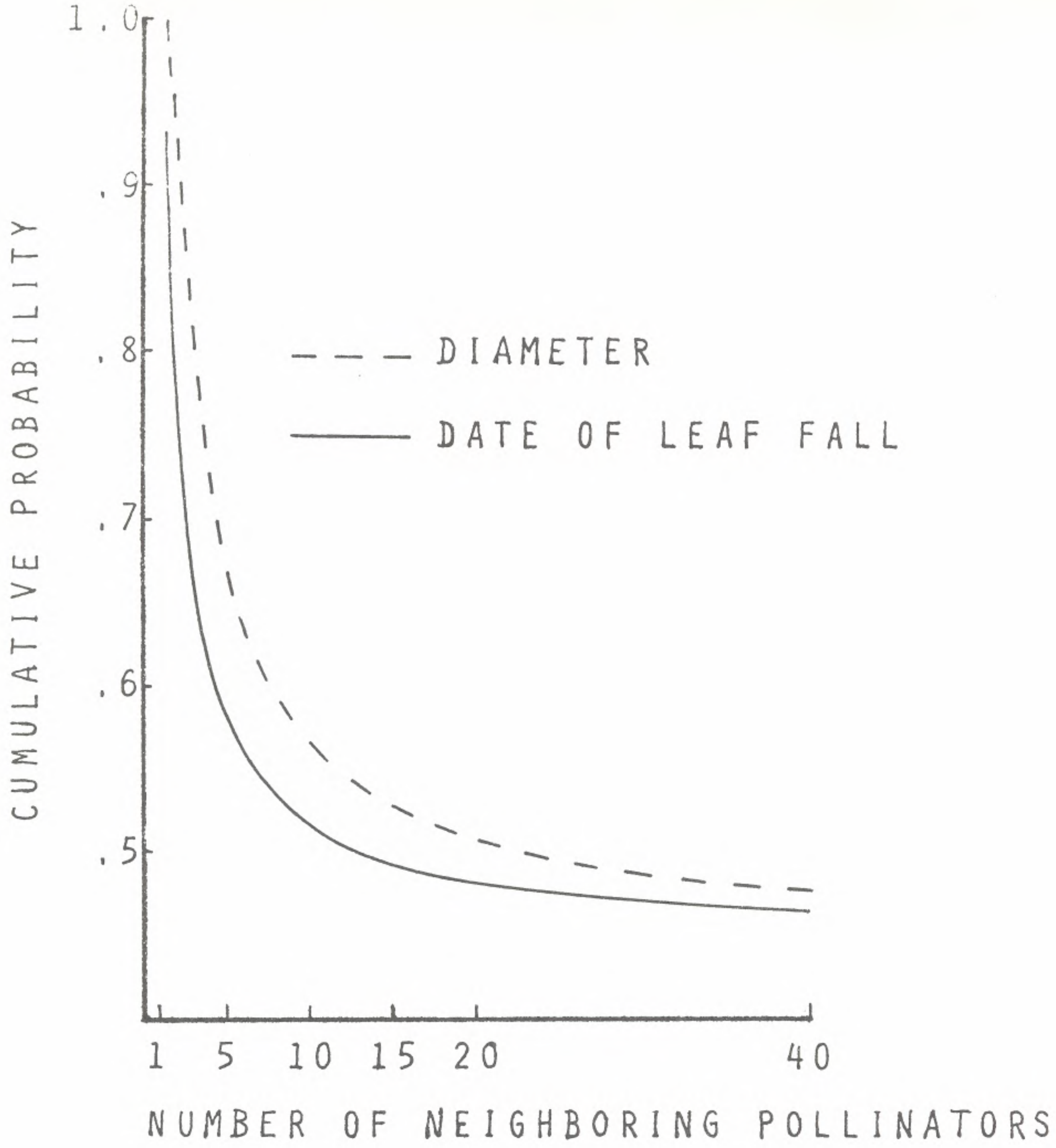

Figure 1.--Cumulative probability of obtaining pollen from more than the indicated number of neighboring pollinators as estimated by diameter and date of leaf fall.

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